RESPIRATORY GAS EXCHANGE AND TRANSPORT IN CRUSTACEANS: ECOLOGICAL DETERMINANTS

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Crustaceans have radiated into many different environments ranging from deep sea hydrothermal vents, through the intertidal zone and freshwater to terrestrial habitats. Adaptation to these varied conditions has included marked and significant changes in both the gas exchange organs and blood pigment function. The functioning of haemocyanin, the respiratory pigment of most crustaceans, is in many species under the complex control of biochemical feed back mechanisms. Modulation of haemocyanin function can occur due to the accumulation of specific metabolites or as a result of specific compounds entering the animal from the environment. For example hydrothermal vent fauna exhibit specific adaptations to high sulphide levels and mesopelagic species containing high levels of ammonia show different but again specific adaptations. Metabolic modulation of blood pigment function occurs most extensively in the sub-littoral and intertidal species. Terrestrial species show the most marked morphological/biochemical changes in the structure and function of the gas exchange organs and appear to have abandoned complex molecular modulation of blood gas transport. The ecological physiology of these adaptive trends is considered using examples, and directions for future investigation are discussed.☐

Crustacean, oxygen, carbon dioxide, haemocyanin, respiratory, gas exchange.

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The study of respiratory gas exchange and transport in crustaceans has proceeded largely on a comparative basis and for practical reasons has dealt primarily with decapod species. As a consequence, our knowledge is disproportionately based on a number of 'large' species from 'interesting or challenging' environments which are then compared to 'normal' species. However, it is by examining adaptations to extremes that the plasticity and adaptability of the Crustacea becomes apparent.

There have been a number of recent reviews that have considered adaptation to specific environments (Powers and Bliss, 1983; Vernberg and Vernberg, 1983; McMahon and Burggren, 1988; Burggren and McMahon, 1988), specific morphological adaptations (Greenaway and Farrelly, 1990) or have given general treatments (Mangum, 1983; Vernberg, 1983; Cameron and Mangum, 1983). The more general papers have not been restricted to respiratory gas exchange and transport.

The present paper, while continuing the basic principle of examining adaptation to extremes and by necessity with a bias towards the decapods, will relate specific adaptations in the gas exchange organs and haemolymph function to the special demands of various habitats. These habitats range from abyssal hydrothermal vents, through the intertidal to fully terrestrial. Often adaptations not directly related to gas exchange and transport have forced compromise on the respiratory physiology. It is not within the scope of this paper to provide a complete description of all species from each habitat. Rather, examples have been selected to demonstrate our current knowledge and to indicate those areas that warrant further study.

DISCUSSION

The two main respiratory gases, oxygen and carbon dioxide, move across the body wall of crustaceans by diffusion. This is often facilitated by a respiratory pigment, most usually haemocyanin, and there is good evidence that CO_2 excretion is aided by carbonic anhydrase (Henry, 1987). Diffusion limited gas exchange can be described by the Fick equation: $M = \frac{K \cdot A}{E} \cdot \delta P$ where M is the amount of diffused gas in $mmol.min^{-1}$, E is the thickness of the barrier and A the area. K is Krogh's diffusion constant ($mmol.min^{-1}.atm^{-1}$) and P is the partial pressure gradient across the barrier. The diffusion constant takes into account not only diffusion through the membrane but also the solubility coefficient of the extracorporeal medium. Since CO_2 is *c.* 25 times more soluble than O_2 in water, diffusion of O_2 rather than CO_2 is the limiting factor in aquatic species. Therefore, it is the maintenance of O_2 supply that is the major modifying factor in the evolution and control of respiratory systems (McMahon and Wilkens, 1983). In air the capacity for O_2 and CO_2 are essentially the same and the outward diffusion of CO_2 therefore relatively slower; which has a major influence on the respiratory gas exchange and transport of air breathing species.

It is generally accepted that in non-malacostracan crustaceans no specialised respiratory structures are present but instead appendages, specialised parts of the integument or the body wall as a whole are employed (McLaughlin, 1983). The simplest form of malacostracan gill is a vascularised lamellar outgrowth of the thoracopod and occurs in multiple pairs in mysids and amphipods. In the isopods these structures are often elaborated (Edney, 1960). The gills of Eucarida are more complex and with few exceptions enclosed within the carapace in the paired branchial chambers through which water (or air) is moved. The most usual arrangement is for water to flow in through openings at the base of pereiopods (Milne Edwards openings) into the hypobranchial space, through the gills into the hyperbranchial space and then pumped out through exhalant openings on either side of the epistome (McMahon and Wilkens, 1983). Primitively, the gills existed as sets of four attached to each appendage but all modern decapods show a reduced number. The gills themselves fall into three categories depending on the complexity of branching: a) phylobranchiate the normal gill type for caridean shrimp and brachyuran crabs; b) trichobranchiate as found in most lobsters and crayfish; and c) dendrobranchiate as found only in penaeoids and sergistoids (McLaughlin, 1983). McMahon and Wilkens (1983) considered that this increased branching of the gills might indicate the evolution of increased surface area for gas exchange.

Perfusion of the gas exchange organs and the respiring tissues is equally important in determining rates of gas exchange. The circulatory system of crustaceans has been termed 'simple' because of the open nature of large parts of the venous system. In the smaller crustaceans this may be true but in the larger decapod species the open circulatory system is complex, highly efficient and tightly regulated (McMahon and Burnett, 1990). Haemolymph-flow through gills has been demonstrated to be organised and the direction controlled (Burggren and McMahon, 1988; Taylor, 1990). Terrestrial species exhibit highly modified gas exchange structures and have made major alterations in perfusion, with respect to breathing air instead of water, or in the case of amphibious species breathing both (see below).

AQUATIC *vs* TERRESTRIAL — A CONTINUUM

The evolutionary and adaptive processes involved in moving from breathing water to breathing air have received some considerable study but it is only recently that we have begun to understand how the Crustacea have accomplished this. The movement of crustaceans into terrestrial environments has occurred either via the freshwater or intertidal zone habitats (Hartnoll, 1988), although in some cases it is unclear which route was followed. Those of direct marine origin tend to have a marine pelagic larval stage whereas those from freshwater benefit from an abbreviated nonplanktonic larval development providing greater independence from water (Hartnoll, 1988). Within this continuum there exist several discrete habitats, marine, estuarine, freshwater, intertidal, tidepool, amphibious, and semi- and fully terrestrial, although any species may not be limited to one.

ESTUARINE/FRESHWATER — SALINITY EFFECTS

The major challenge for species moving into estuarine habitats and from there progressively to freshwater is the maintenance of salt balance. Increased osmoregulatory work could theoretically lead to increased gas exchange but this has been difficult to demonstrate (Taylor, 1988). Moving into freshwater and more especially environments of varying salinity does, however, have some demonstrable effects (Vernberg, 1983; Cameron and Mangum, 1983; Taylor, 1988). The green shore crab *Carcinus maenas* is a typical estuarine/intertidal species. The normal estuarine, intertidal and rock pool environments are subject to frequent and often abrupt changes in salinity. After exposure to low salinity the respiration rate of *C. maenas* is significantly elevated, peaking after 3–4 h but remains elevated for several days (Taylor, 1977). This response appears to be standard for those species so far investigated (Taylor, 1988). Quite clearly there is no rapid acclimation to reduced salinity.

The increased oxygen uptake is associated with a hyperventilatory response; with the increased oxygen demand possibly being met by a tachycardia and increased cardiac output (Taylor, 1977, 1988).

The oxygen transporting properties of the haemocyanin from a number of estuarine and intertidal animals respond to salinity changes (*Carcinus maenas*, Truchot, 1973; *Callinectes sapidus*, Weiland and Mangum, 1975). These changes can occur as a result of the failure to completely regulate blood ions with respect to changing environmental salinity. In most aquatic crustaceans, such as *Carcinus*, increases in the concentrations of Ca and Mg especially, induce increased affinity for O_2 by the haemocyanin and also increase the Bohr shift (Fig. 1). The rock pool species *Palaemon elegans* shows good ion regulation and consequently no effect on oxygen affinity when exposed to low salinity (Ramirez de Isla Hernandez and Taylor, 1985; Taylor *et al.*, 1985). *Callinectes sapidus* although an osmoregulator also shows a decrease in the oxygen affinity of Hc when acclimated to low salinity and this led Mason *et al.* (1983) to suggest that some small dialysable factor may be responsible. Recently it has be shown, however, that *C. sapidus* exhibits changes in haemocyanin phenotype, the expression of which is dependent on salinity (Mangum and Rainer, 1988), and the phenotypes have different functional characteristics.

These changes with respect to acclimation salinity do not, however, always elicit the same effect *in vivo* due to concomitant changes in blood pH. Low salinity results in an increased blood pH and therefore an increase in oxygen affinity which compensates for the decreased affinity due to lowered blood ions (Fig. 1) (Truchot, 1973). There is also good evidence that some species show increased Hc levels in response to acclimation to low salinity (Sabourin, 1984; Taylor *et al.*, 1985) but this occurs slowly over a number of days and is primarily an osmoregulatory response and not respiratory.

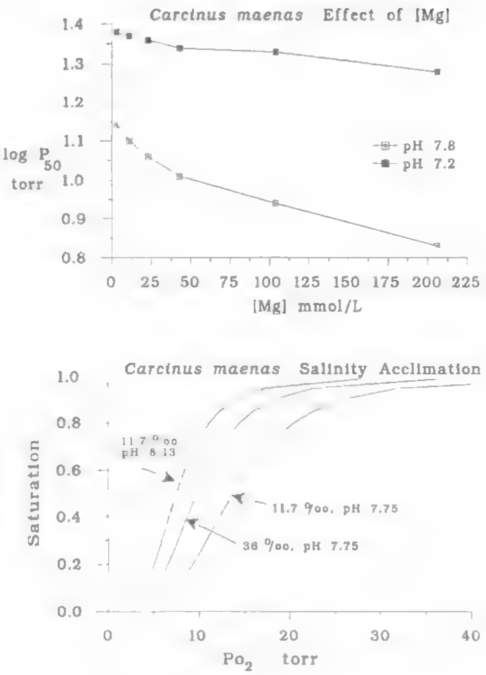


FIG. 1. Upper, The effect of Mg on the oxygen affinity (log P_{50}) of haemocyanin from *Carcinus maenas*. The increase in affinity due to higher Mg concentration is more marked at high pH. The increased divergence of the plots at pH 7.2 and pH 7.8 is due to the increased pH sensitivity, i.e. greater Bohr shift, induced by high Mg levels (after Truchot 1975);Lower, Salinity acclimation of O_2 transport in *C. maenas*. The centre curve indicates the oxygen equilibrium of blood from *Carcinus* in full strength seawater and at the *in vivo* pH. Maintaining blood pH at 7.75 but reducing salinity would reduce affinity as shown by the right curve. Salinity acclimation is normally accompanied by an increase in blood pH which compensates for the reduced affinity to actually produce a slight increase in affinity under *in vivo* conditions (left curve). Curves constructed from the data of Truchot (1973).

SUBLITTORAL

The most common demand on the respiratory system of sub-littoral species is to maintain aerobiosis during exercise. Exercise has been used as experimental treatment by a number of workers and extensive data exist for various *Cancer* species. In *C. magister* 20 min exercise causes an increase in ventilation and perfusion (McMahon *et al.*, 1979). The increase in scaphognathite and heart beat rates is accompanied by a marked increase in oxygen uptake which is reflected in a decrease of the blood oxygen content (Fig. 2). In a parallel study (McDonald *et al.*, 1979) it was noted that 20 min exercise resulted in significant L-lactate (end product of anaerobiosis) efflux into the blood, with a significant acidosis and a rise in the partial pressure of CO_2, the latter despite the hyperventilation (Fig. 2). The anaerobic component of this response, i.e. the elevated lactate levels and the acidosis, continued to increase for some 30 min post exercise and before

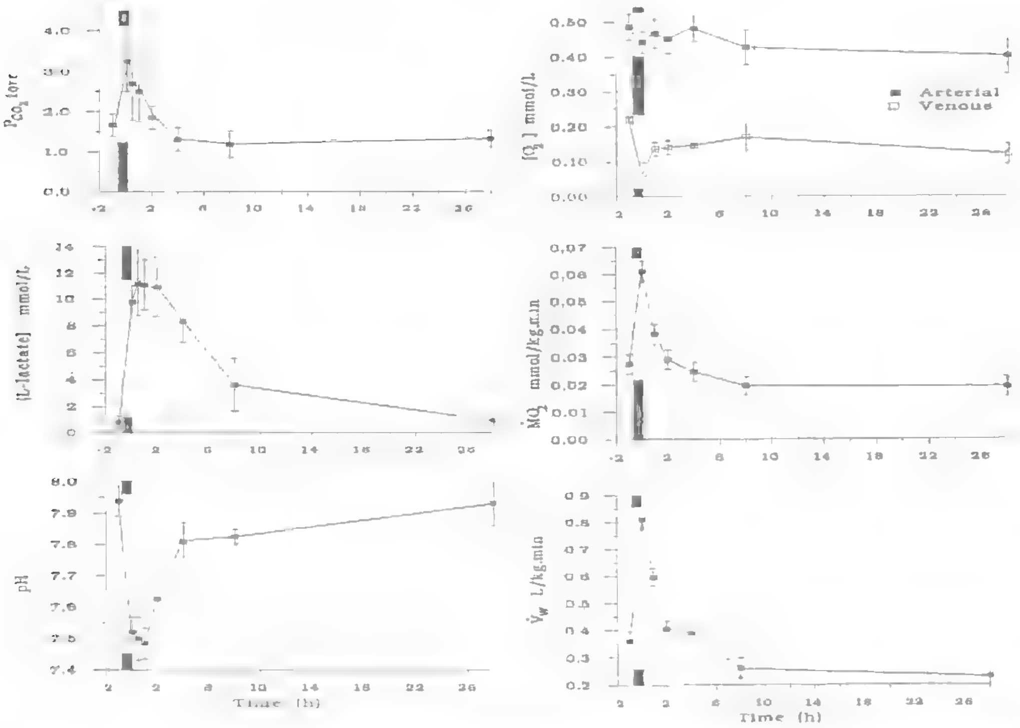


FIG. 2. Changes in respiratory blood-gas parameters, lactate and pH, oxygen uptake and ventilation volume during 20 min exercise (filled vertical bars) and 24 h recovery in *Cancer magister*. Arterial and venous blood values are supplied for O_2 content (data abstracted from McDonald *et al.*, 1979; McMahon *et al.*, 1979).

returning to normal resting values. Complete recovery of all parameters required 24 h (Fig. 2). Obviously the exchange of respiratory gas and/or transport is insufficient to maintain aerobiosis in the working muscles and supplementary anaerobic energy production is used to meet the increased demand.

Some species, normally sublittoral, contain individuals that become air exposed and the success of these individuals in breathing air may determine their survival. Small *Cancer productus* (<100g) are often found emersed in the low intertidal zone (DeFur and McMahon, 1984a). Air exposure of *Cancer* elicits a different response from exercise in that there is a decrease in oxygen uptake due to the failure of the gills as gas exchange organs but there is a similar increase in ventilation, in PCO_2 and also CO_2 content (Fig. 3) (DeFur and McMahon, 1984a,b). The response to this shortfall in oxygen supply is again the initiation of anaerobiosis and the efflux of L-lactate into the haemolymph which exacerbates the haemolymph acidosis (Fig. 3). It is important to note that attempts to compensate for this acidosis appear to involve the mobilisation of $CaCO_3$ from the carapace to produce HCO_3- (Henry *et al.*, 1981; DeFur and McMahon, 1984a; Innes *et al.*, 1986). The concomitant increase in circulating Ca will tend to have a potentiating effect on the affinity of the Hc for oxygen (see above) partially compensating for the decreased affinity due to the Bohr shift and thereby assisting oxygen loading at the gills. Again complete recovery of all parameters, especially L-lactate, required at least 24 h. Air exposure of aquatic species appears, therefore, not to be met with any special adaptive response. L-lactate may mitigate some of the effects of air exposure. Truchot (1980) reported that L-lactate increased the oxygen affinity of some crustacean haemocyanins, including *Cancer*. This effect has now been substantiated for a number of species (Bridges and Morris, 1985; Morris, 1990; discussed below). The immediate benefit would seem to be a partial compensation for the effect of a metabolic acidosis, which reduces the affinity of haemocyanin for O_2. Depending on circumstances the effect can either improve loading of oxygen at the gills or increase the size of the venous reserve, that is the amount of oxygen remaining bound to Hc after passing through the tissues (Morris, 1990). The latter would seem to be an adaptation to exercise and the former to breathing hypoxic water.

LITTORAL AND POOL ENVIRONMENT

Within the littoral zone exist a number of microhabitats of which the rock pool environment is perhaps the best studied. While conditions in the pools may be similar to those of inshore seawater they can frequently and regularly become extreme, with wide fluctuations in oxygen availability (PO_2 10 – 500 torr), temperature (-1.5 – 30°C), salinity, pH and carbon dioxide levels (Truchot and Duhamel-Jouve, 1980; Morris and Taylor, 1983). Similar environmental changes have been described for habitats on boulder and sedimentary shores (Agnew and Taylor, 1986 and citations therein). With the exception of salinity similar environmental stresses occur in freshwater bodies.

The rate of gas exchange and transport is determined by the metabolic demands of the animal, which in crustaceans with no temperature homeostasis will tend to vary with environmental temperature. The fluctuating temperatures experienced in smaller bodies of water might be expected to have significant effects on metabolic requirements. Long term (seasonal) temperature changes may be met by temperature acclimation (Newell, 1979). The pool dwelling prawn *Palaemon elegans*, which shows temperature acclimation over a period of weeks, exhibits greater thermal tolerance (survives < 0°C) than the open water species *P. serratus* and *P. adspersus* which avoid temperature extremes (Taylor, 1988). In addition to greater tolerance such species often show some metabolic independence of temperature ($Q_{10} < 2.0$). Fluctuating temperatures are a feature of the littoral zone generally and are reflected in intertidal hermit crabs by low Q_{10}'s of 1.4 and 1.6 (Burggren and McMahon, 1981). Similarly low Q_{10}'s were recorded for *P. elegans* but these were size dependent (Morris and Taylor, 1985a). The increased O_2 demand and CO_2 production is met by increased ventilation and perfusion together with changes in the transport properties of the blood. Oxygen transport is affected by reduction in dissolved O_2 at high temperature and by changes in the haemocyanin O_2 affinity, which arise from allosteric modulation and temperature dependent changes in pH (~ -0.016 pH.°C^{-1}). Generally, the effect of increased temperature, at constant pH, is to decrease O_2 affinity (Mangum, 1983). Acclimation of Hc oxygen affinity also seems possible. *In Carcinus* moved to a higher temperature oxygen affinity first decreased but then slowly increased, which Truchot (1975) suggested was due to an increase of a dialysable factor. Moving *Hemigrapsus nudus*, an amphibious intertidal crab, from 15 to 30°C caused urate concentrations to increase from 0.015 to 0.052 mmol.L^{-1} (Morris, Greenaway and McMahon, unpubl.). Urate has been identified as a modulator of Hc O_2 affinity (below) and may explain the above temperature effects on *Carcinus*, the haemocyanin of which is sensitive to urate (Lallier and Truchot, 1989a). This decreased O_2 affinity at higher temperature may compromise oxygen uptake, although unloading at the tissues might be enhanced. In rock pool species this is mitigated by the fact that the highest temperatures occur during periods of hyperoxia (Morris and Taylor, 1983). Conversely, hypoxia is associated with the lowest diel temperatures and reduction in oxygen demand. Apart from allosteric modulation the haemocyanin of many intertidal species shows reduced temperature sensitivity at temperatures near the environmental mean. Crustacean Hc normally exhibits a δH of -35 kJ.mol^{-1} or larger, δH being the change in the heat of oxygenation of Hc with an increase in temperature. For example in *P. elegans* δH = -1.7 kJ.mol^{-1} (Morris *et al.*, 1985) and the hermit crab *Pagurus bernhardus* δH = 0 to -18 kJ.mol^{-1} (Jokumsen and Weber, 1982). Both of these species have Hc that is especially sensitive to pH ($\phi << -1.0$) which supports the suggestion that there is an inverse correlation between pH sensitivity and temperature sensitivity (Burnett *et al.*, 1988), although this seems not to be true for all species, e.g. terrestrial and hydrothermal vent species (see below). It could also be argued that those species living under a relatively constant temperature regimen exhibit no special adaptation to temperatures never encountered, and that reduced sensitivity is a response to a eurythermal environment.

During hypoxia many crustaceans can maintain a near constant oxygen consumption down to very low levels of environmental oxygen and are termed regulators (Fig. 4). Below this 'critical' PO_2 anaerobiosis becomes increasingly important. The critical PO_2 (Pc) is highly variable between species but it now appears that the Pc is correlated with the extent and duration of hypoxia experienced (Table 1). The maintenance of MO_2 is due to a response common to nearly all species investigated, a pronounced increase

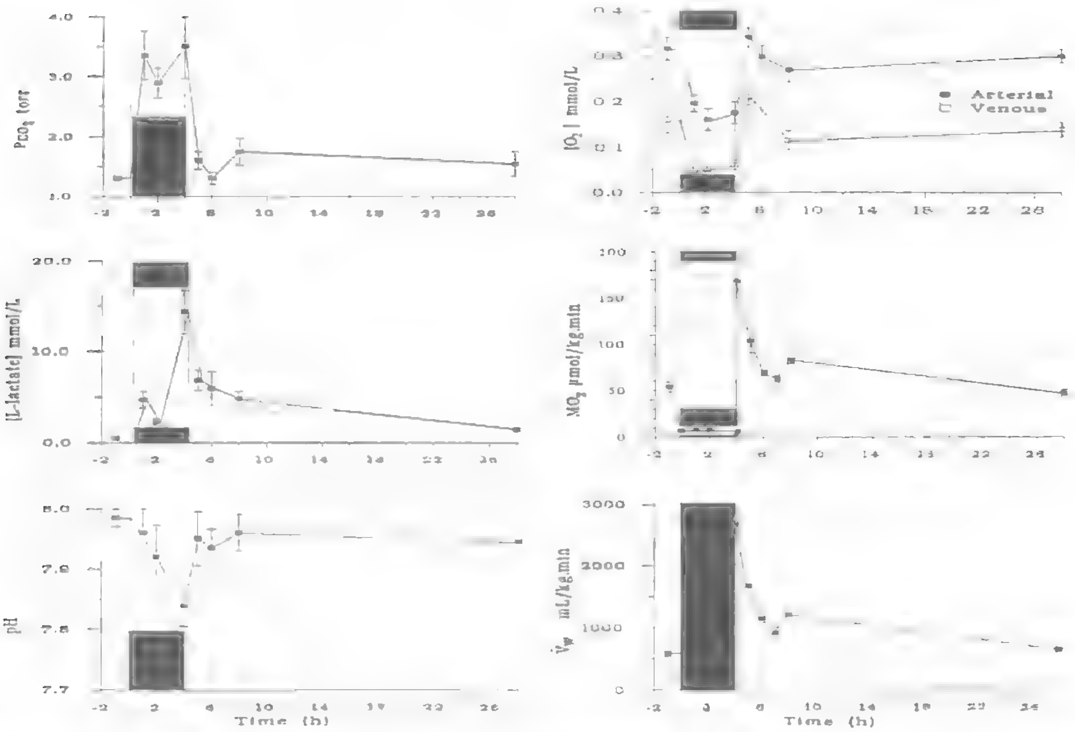


FIG. 3. Changes in respiratory blood-gas parameters, lactate and pH, oxygen uptake and ventilation volume during 4 h air exposure (filled vertical bars) and 24 recovery in *Cancer productus*. Arterial and venous blood values are supplied for O_2 content (data abstracted from DeFur and McMahon, 1984a,b).

in the rate of scaphognathite beating (Taylor, 1988). The rate of beating increases steadily until the Pc is reached, e.g. *P. elegans* (Fig. 4). Although this increased ventilation helps maintain oxygen uptake the increased work itself represents a metabolic demand and at the Pc it is considered that O_2 uptake is sufficient only to supply the pumping activity.

Taylor (1988) compares rock pool and open water species and concludes that rock pool species often show higher Hc concentrations, which increases the amount of O_2 transported, and additionally that these Hcs show high affinity and pH sensitivity. The high affinity would encourage oxygen uptake at the gills and the latter could assist in unloading at the tissues. While Hc concentration certainly is a factor it is now apparent that intertidal species, including rock pool animals have a series of mechanisms for 'fine tuning' Hc oxygen affinity (Morris, 1990). As a consequence the affinity will vary in dependence of physiological condition. The Hc of *Palaemon elegans* for example is extremely sensitive to L-lactate and affinity is markedly increased with only small changes in concentration (Table 2). The most apparent advantage of this effect is to aid the loading of oxygen at very low ambient oxygen and prevent the rapid onset of extensive anaerobiosis.

In addition to L-lactate it has been found that urate (Morris *et al.*, 1985a,b) and more recently the catecholamine, dopamine (Morris and McMahon, 1989) have marked potentiating effects on some crustacean Hcs. In *Carcinus* and the prawn *Penaeus japonicus*, which encounters hypoxic conditions in lagoons, urate accumulates in the blood with hypoxia (Lallier and Truchot, 1989a,b). In addition, blood urate levels decrease progressively as the ambient PO_2 is increased into the hyperoxic range (Lallier *et al.*, 1987). Clearly urate concentration responds to environmental oxygen levels above the Pc whereas L-lactate formation is significant below the Pc, leading Lallier and Truchot (1989a) to conclude that under normal circumstances urate is most important in regulating blood oxygen affinity. Neurohormonal modulation of pigment oxygen affinity is most likely in situations of sudden stress. Intertidal, rock pool and near shore species appear to be provided with a suite of complementary biochemical feedback systems for regulating oxygen transport (Morris, 1990).

The blue crab *Callinectes sapidus* is also occasionally found in the intertidal zone, although it copes poorly with breathing air, and contains Hc sensitive to L-lactate and urate. Prolonged hypoxia (50–55 torr) results in enhanced blood oxygenation but not as a result of significant increases in either lactate or urate but rather due to increase in circulating Ca and by a change in the Hc phenotype (DeFur *et al.*, 1990).

The transport of CO_2 will also be affected by the above modulators since the transport of CO_2 and O_2 are linked under most circumstances (Bridges and Morris, 1989). Hypoxia in rock pools is invariably accompanied by hypercapnia, with the inverse relationship during hyperoxia, a feature which has not been rigorously duplicated in laboratory simulation studies. Simultaneous variation in CO_2 and O_2 levels in rock pools has markedly different consequences than varying O_2 alone (Bridges and Morris, 1989). Using artificial tide pools Truchot (1986) demonstrated that the blood alkalosis observed during laboratory hypoxia, as result of the hyperventilatory response, is much less obvious when the CO_2 level in the water concomitantly increases. Similarly the acidosis often observed as a result of hypoventilation during hyperoxia is considerably ameliorated. Thus rock pool animals face significantly different demands on the oxygen transport system than do species inhabiting hypoxic oceanic waters such as the oxygen minimum layer (see below).

When water PO_2 falls below the Pc many species show an important behavioral response, partial emersion. Although *P. elegans* exhibits exceptional oxyregulation, below 20 torr the prawns will partially emerse themselves at the air–water interface and by a combination of hyperventilation and pleopod beating aerate the surface film (Taylor and Spicer, 1988). Similar behaviour has been observed for freshwater crayfish, *Orconectes rusticus* (McMahon and Wilkes, 1983). This behaviour under conditions of hypoxia close to the Pc increases haemolymph oxygenation but also allows CO_2 exchange with the water, which maintains blood pH (Taylor and Spicer, 1988). Similarly, small *Cancer productus* when air exposed *in situ* where they are often partially buried take advantage of the interstitial water to reduce the degree of internal hypercapnia and acidosis (Fig. 3). Under conditions of severe hypoxia (< Pc) many of these normally obligate water breathers emerge completely from the water, e.g. *P. elegans* (Taylor and Spicer, 1988) and *Echinogammarus pirloti* (Agnew, 1985). This response, whereby under extreme conditions it is more beneficial to breathe air than water, may represent selective pressure directing some species towards an amphibious existence.

AMPHIBIOUS – AIR AND WATER BREATHING

The amphibious Crustacea, both those from the supratidal and those from freshwater bodies, show varying degrees of independence from water. This may be viewed as an evolutionary trend with species such as *Carcinus maenas* (Taylor and Butler, 1978) and the crayfish *Austropotamobius pallipes* (Taylor and Wheatly, 1981) at the more aquatic end. *A. pallipes* is exemplary in that when the freshwater that it inhabits becomes very hypoxic it moves into air (Taylor and Wheatly, 1981). This initially promotes a response similar to that exhibited by *C. productus* (Fig. 3) but during a 24 h emersion period the initial increase in blood lactate and subsequently Ca appear to maintain oxygen up-

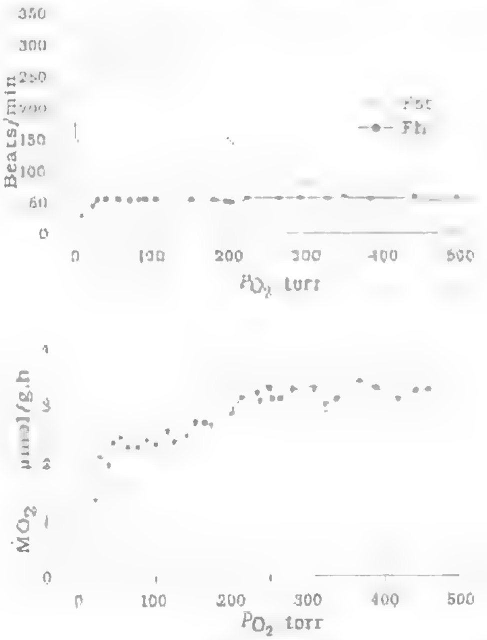


FIG. 4. Showing the regulation of $\dot{M}O_2$ (lower panel) by *Palaemon elegans* over a wide range of oxygen availability. Oxyregulation ceases at *ca.* 20 torr the critical PO_2 for this species. The upper panel shows regulation of heart rate (Fh) by *P. elegans* and the scaphognathite rate (Fsc) during hypoxia. The hyperventilatory response ceases near the critical PO_2.

TABLE 1. Critical oxygen partial pressures (Pc) for the regulation of oxygen consumption in selection of crustaceans from various habitats.

Species	Pc (torr)	Source
Cancer pagurus	20–40	Bradford and Taylor, 1981
Carcinus maenas[1]	60–80	Taylor (1976), Jouve and Truchot (1978)
Pachygrapsus crassipes	50	Burke (1979)
Austropotamobius pallipes	40	Wheatly and Taylor (1981)
Upogebia pugettensis[2]	45–50	Thompson and Pritchard (1969)
Callianassa californiensis[2]	10–20	Thompson and Pritchard (1969)
Palaemon adspersus	70	Hagerman and Weber (1981)
Palaemon elegans[3]	10–15	Morris and Taylor (1985b)
Palaemon serratus	50–60	Taylor (1988)
Palaemonetes varians	10–15	Hagerman and Uglow (1984)
Echinogammarus pirloti[1]	15–25	Agnew and Taylor (1985)
Echinogammarus obtusatus[1]	15–25	Agnew and Taylor (1985)
Hemigrapsus nudus[1]	<10	Morris *et al.* (In Preparation)
Gnathophausia ingens[1]	6	Childress (1975)
Acanthephyra curtirostris[4]	8	Childress (1975)
Euphausia pacifica[4]	18	Childress (1975)
Bythograea thermydron[5]	14[a], 9[b]	Mickel and Childress (1982b)

[1]Intertidal/interstitial species. [2]Intertidal burrowing species. [3]Primarily rockpool species. [4]Midwater species from the oxygen minimum layer, [5]Hydrothermal vent crab [a]Measured at 8–25°C, [b]Measured at 2°C; Species not numbered are normally aquatic/open water forms.

take and transport, and stabilise blood pH and $P\mathrm{CO_2}$ (Taylor and Wheatly, 1981; Morris *et al.*, 1986b). The L-lactate produced in the initial period of hypoxia is slowly removed from the blood (Taylor and Wheatly, 1981). *A. pallipes* employs the same basic responses as fully aquatic species and this seems adequate for several days of air breathing. Compared to obligate aquatic species (*Liocarcinus*, Johnson and Uglow, 1985) *Carcinus* shows morphological adaptations in that the gills are more strongly chitinised and thus have a lesser tendency to collapse in air, allowing some gas exchange to occur across the gills.

Hemigrapsus nudus, a more truly amphibious species, spends the greater part of the day breathing air but shows no specific modification to the gills, which collapse and adhere when the crab enters air. Instead this species shows increased vascularisation of the membrane lining the branchial chamber which takes on a lung function. For example in *H. nudus* breathing air for 4 hours the venous blood oxygen content was 0.20 mmol.L^{-1} and that of the arterial blood 0.26 mmol.L^{-1}, while blood exiting the lung contained 0.30 mmol.L^{-1} oxygen (~75% saturated; Morris, Greenaway and McMahon, unpubl.). Quite clearly oxygen rich blood from the pulmonary circuit was being diluted by oxygen poor blood from the branchial circuit. Interestingly, *Hemigrapsus* Hc shows little sensitivity to lactate (Table 2) indicating a reduced dependence on modulation of respiratory pigment function, indeed air breathing by *Hemigrapsus* causes no significant lactate production (Morris, Greenaway and McMahon, in prep). In the absence of biochemical modulation of haemocyanin function *Hemigrapsus* maintains a constant arterial-venous oxygen content difference, a stable pH and a stable, if elevated blood CO_2 near 3.5 torr (Fig. 5). Amphibious species differ from aquatic species in that the blood gas and acid-base parameters during air breathing are stabilised and respiration is not significantly supplemented by anaerobiosis.

A number of amphibious species have developed unusual accessories to breathing air. These include the evolution of gas exchange windows in the merus of each walking leg of *Scopimera* (Maitland, 1986) and the visceral 'lung pump' of *Holthuisana* (Greenaway and Taylor, 1976). *Holthuisana*, in reality a semi-terrestrial crab, while breathing air ceases scaphognathite activity and instead moves the internal viscera from side to side alternately occluding and opening the branchial spaces and thereby causing a ventilatory current over the gas exchange surfaces. It is of note that while species such as *Hemigrap-*

TABLE 2. The oxygen affinity as P_{50}, its sensitivity to L-lactate and urate for some crustaceans selected with respect to habitat and mode of existence. Values assessed at the species' normal environmental temperature.

Species	P_{50}(pH7.8) (1mmol/L lactate)	$\frac{\delta \log P_{50}}{\delta \log[\mathrm{Lac}]}$	$\frac{\delta \log P_{50}}{\delta \log[\mathrm{urate}]}$	ϕ	Source
Palaemon elegans[1]	12.5	-0.56		-1.4	Bridges and Morris (1985)
Apohyale pugettensis[1]	16.1	-0.46		-1.67	Spicer and McMahon (1990)
Traskorchestia traskiana[3]	24.8	-0.30		-0.70	Spicer and McMahon (1990)
Bythograea thermydron[6]		-0.27		-0.3 -1.5	Sanders and Childress (Pers Com.)
Cancer pagurus[2]	14.3	-0.21		-0.86	Truchot (1980)
Callinectes sapidus[2]	6.1	-0.21	-0.11	-1.14	Booth *et al.* (1982), Bridges and Morris (1985), deFur *et al.* (1990)
Uca pugilator[3]	8.9	-0.20	0	-1.67	Byrne, Morris, Spicer and McMahon (Unpub.)
Cancer magister[2]	8.9	-0.19	-0.07	-1.03	Morris and McMahon (1989)
Acanthephyra smithi[4]	3.9	-0.17		-0.7	Sanders and Childress (1990a)
Gnathophausia ingens[4]	1.6	-0.13		-0.8	Sanders and Childress (1990b)
Carcinus maenas[1,3]	10.9	-0.10	-0.22	-0.55	Truchot (1980), Lallier and Truchot (1989a)
Austropotamobius pallipes[5]	3.9	-0.19	-0.39	-0.46	Morris *et al.* (1986a), Morris *et al.* (1985a)
Hyas coarctatus[2]	24	-0.17		-0.3 -0.7	Morris and Bridges (1989)
Ocypode saratan[7]	15.1	-0.16		-0.67	Bridges and Morris (1985)
Megalorchestia californiana[3,7]	14.7	-0.10		-0.78	Spicer and McMahon (1990)
Penaeus japonicus[a]	2.8 (1.41)[b]	-0.08	-0.03	-1.5	Lallier and Truchot (1989b)
Hemigrapsus nudus[7]	7.1	-0.06	-0.09	-0.7	Morris, Greenaway and McMahon (Unpub.)
Acanthephyra acutifrons[4]	5.2	-0.06		-0.88	Sanders and Childress (1990a)
Glyphocrangon vicaria[4]	2.5	-0.04		-0.37	Arp and Childress (1985)
Oplophorus gracilirostris[4]	5.6	-0.03		-0.66	Sanders and Childress (1990a)
Talitrus saltator[7]	17.6	-0.03	0	-0.75	Spicer, Taylor, McMahon (1990)
Holthuisana transversa[7]	4.9	0		-0.13	Morris *et al.* (1988a)
Geograpsus crinipes[8]	16.6	0	0	-0.53	Morris, Greenaway, McMahon and Sanders (In Prep)
Gecarcoidea natalis[8]	15.1	0	0	-0.38	Morris, Greenaway, McMahon and Sanders (In Prep)
Gecarcoidea lalandii[8]	12.0	0	0	-0.55	Morris, Greenaway, McMahon and Sanders (In Prep)
Birgus latro[8]	7.9	0	0	-0.68	Morris *et al.* (1988b)
Coenobita clypeatus[8]	7.2	0		-0.43	Morris and Bridges (1986)

#Values calculated using author's coefficients, [a]Lagoon species values for pH 7.6. [b]Extrapolated to pH 7.8
[1]Rockpool, [2]Sublittoral, [3]Intertidal, [4]Pelagic, [5]Freshwater. [6]Hydrothermal vent, [7]Amphibious/Semi-terrestrial, [8]Terrestrial

sus are good oxyregulators with a low Pc (Table 1). *Holthuisana* shows no obvious Pc and is an oxyconformer (Greenaway *et al.*, 1983b) and presumably elects to breathe air whenever the water becomes hypoxic. A further interesting adaptation to bimodal breathing by *Holthuisana* is the facultative switching of blood flow from the gills (water breathing) to the lungs (air breathing); the ratio being 1:6.6 in favour of lungs while in air and 1:4.1 in favour of gills in water (Taylor and Greenaway, 1984). This phenomenon almost certainly occurs in other species but it remains to be demonstrated. Other bimodally breathing species such as *Cardisoma* show well developed lungs and are equally facile at breathing air as water (McMahon and Burggren, 1988) but appear to be dependent on water for ion and osmoregulatory reasons (Greenaway, 1989).

TERRESTRIAL — AIR BREATHING

A number of adaptive features exhibited by the more accomplished air-breathing amphibious species are characteristic of and considerably more developed in terrestrial species. Further modification of the gills to aid in air-breathing occurs in a number of species, e.g. *Ocypode* *(Greenaway and Farrelly, 1984)*. Most air-breathing species however, show reduction in gill area and extensive elaboration of the branchiostegal lining for gas exchange (Fig. 6). In *Birgus latro* the gills take no part in oxygen uptake (Greenaway *et al.*, 1988). Although crustacean lungs have assumed varying forms data from several species indicate that the lungs are very efficient in O_2 uptake, in part due to the attenuation of the epithelial cells and chitin layer (McMahon and Burggren, 1988; Greenaway and Farrelly, 1990). For example in 4 of 5 disparate species of air breathing crab Greenaway and Farrelly (1990) found that the pulmonary blood contained significantly more oxygen than the pericardial blood and the difference could be as much as 35% more, indicating that lungs are more important than gills. Indeed the most terrestrial species have become obligate air breathers and when immersed in water become increasingly anaerobic due to the reduction in oxygen diffusion at the exchange surface, e.g. *Gecarcinus lateralis* (Taylor and Spencer-Davies, 1982). Similar observations have been made for terrestrial amphipods (Spicer and Taylor, 1987). The evolution of lungs has also led to increased arterial PO_2 in some cases significantly greater than 100 torr (*Pseudothelphusa*, Innes *et al.*, 1986; *Birgus*, Greenaway *et al.*, 1988), indicating that in resting animals the physically dissolved O_2 supplies a significant part of the oxygen demand of the animal.

One considerable advantage in breathing air is the relatively greater oxygen content (57mmol.L^{-1}.torr^{-1}) compared with water (1.8 — 2.2 mmol.L^{-1}.torr^{-1}) which together with a much reduced kinematic viscosity (~8%) can make extracting oxygen from air considerably less expensive. As a consequence there is a tendency to make energetic savings by reducing the rate of ventilatory pumping, without reducing oxygen uptake (Table 3). Many amphibious species show markedly different rates in air and water (Table 3).

Relatively elevated PCO_2 in the blood is the normal condition for air breathers and is a consequence of the parameters of the Fick equation (see above). For air breathing species the reduced ventilation with respect to environmental oxygen availability will exacerbate problems of CO_2 excretion. Movement of CO_2 out of the animal into air requires a greater diffusion gradient and therefore higher internal PCO_2 values. There is some evidence that ventilatory drive may become increasingly CO_2 sensitive in terrestrial species (McMahon and Burggren, 1979). The excretion of CO_2 may occur across the lungs as well as the gills and appears to be facilitated by carbonic anhydrase (CA) which catalyses the $CO_2 \leftrightarrow HCO_3^-$ reaction, thereby accelerating the diffusion of CO_2 from the blood and into the epithelial cells of gas exchange organs. While the amphibious *H. nudus* has significant but low levels of CA in its lungs the terrestrial *Birgus* has CA at >25% the specific activity of the gills which may explain the measurable CO_2 loss from the blood passing through the lungs (Morris and Greenaway, 1990). The high CO_2 levels in terrestrial species does not result in a noticeably lower blood pH *cf.* aquatic species. This may be in part because of the usually higher Hc concentrations (for values see McMahon and Burggren, 1988) which may exceed 00 mg.mL^{-1} in some land crabs.

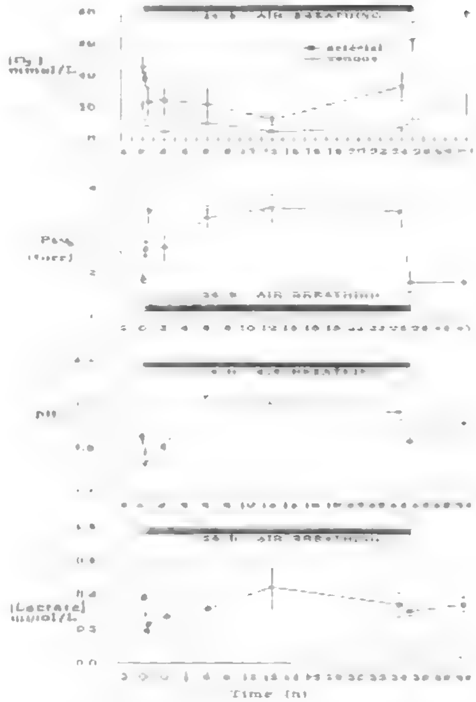


FIG. 5. Respiratory gas parameters, pH and [L-lactate] measured in the blood of *Hemigrapsus nudus* before, during and for 6 hours after 24 h air breathing (indicated by horizontal bars). Arterial and venous O_2 content is given (Morris, McMahon and Greenaway, unpubl.).

The high concentrations of Hc in the blood of most terrestrial species has been interpreted as increasing oxygen supply to the tissues (McMahon and Burggren, 1988) and while this is important during any sustained exercise the efficacy of the lungs together with Hc O_2 affinity

(Table 2) ensures that dissolved O_2 makes an important contribution. During exercise the Hc oxygen saturation in *Birgus* falls from 100% arterial and ~60% venous to only 80% and 25% by which time L-lactate concentrations have risen to over 22 mmol.L^{-1} (Greenaway *et al.*, 1988), indicating that the O_2 limiting step is diffusion from the blood into the mitochondria.

In more than 20 species of terrestrial decapod studied the haemocyanin shows no significant sensitivity to L-lactate or urate (Table 2). Indeed there appears to be a trend for increased air-breathing to be correlated with lower sensitivity. The result is that the allosteric modulation of Hc oxygen affinity used by aquatic organisms to optimise O_2 delivery during exercise or environmental hypoxia, or by proto-amphibious species to temporarily stabilise blood gas transport during forays into air, is not utilised by well adapted air-breathing species. Instead the low kinematic viscosity and high O_2 content of air appears to make compensation *via* changes in ventilatory and heart rates more economical. A further consideration is that urate is the prime nitrogenous waste in at least one species (*Birgus latro*) and accumulates as solid in the body of this and other terrestrial species (Greenaway and Morris, 1989; and citations therein). Urate solutions are saturated at low concentration and presumably there is no advantage in selecting for an effector substance which is always at maximum concentration.

The Hc of terrestrial species appears to be characterised by low pH sensitivity, the small Bohr shifts being approximately 50% the magnitude found for rock pool species (Table 2). The immediate consequence of this is that the effect of very large mixed acidosis (PCO_2 and L-lactate increase) often < pH 7.0 e.g. *Birgus latro* (Greenaway *et al.*, 1988) on Hc oxygen affinity is minimised. There have been several suggestions of a correlation between terrestriality and Hc O_2 affinity but a consideration of data collected at the species normal environmental temperature (and constant [lactate]) indicates no trend (Table 2). The problem is complicated by the modulator sensitivity of Hc in many aquatic species. The only modulating substance of note in terrestrial species would appear to be Ca which may vary in response to drinking water quality, moult stage or during exercise induced acidosis. Values for log $\delta P_{50}/\delta \log$ [Ca] for water breathers range from -0.28 for *Carcinus* (Truchot, 1975) to -0.82 *Callinectes* (Mason *et al.*, 1983). This coefficient varies from near 0

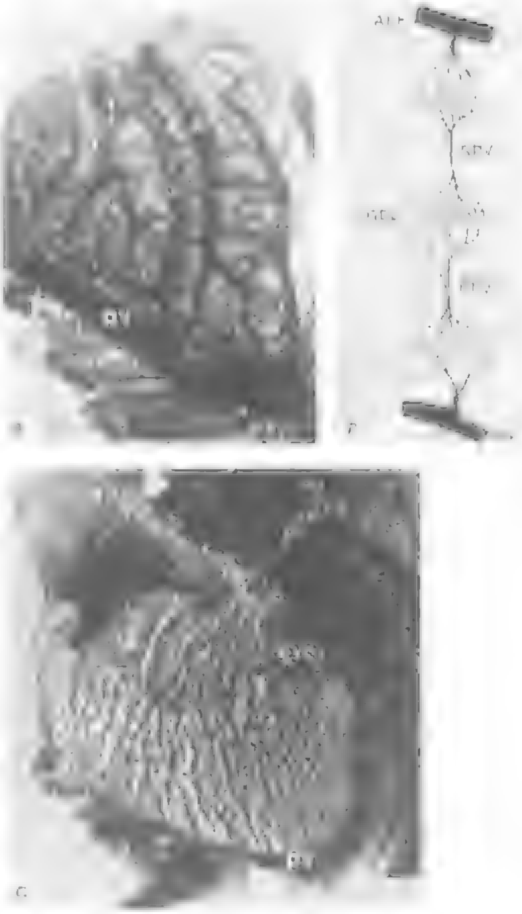


FIG. 6. Crustacean lungs. A, Corrosion cast of part of the vasculature of the lung of *Ocypode cordimanus*. Note the single set of vessels (A), which interdigitates with the efferent vessels (E). Haemolymph returning from the lung is collected by a pulmonary vein (pv), which opens into the pericardial cavity. B, Diagrammatic illustration of the pattern of haemolymph flow through the lungs in terrestrial crabs of the families Gecarcinidae, Grapsidae and Sundathelphusidae. Afferent haemolymph passes to the respiratory membrane three times before reaching the pulmonary veins. AFF, Afferent vessel; GEL, gas exchange lacunae; RPV, respiratory portal vein; PV, pulmonary vein. C, Corrosion cast of the vasculature of one lung of the terrestrial crab *Geograpsus grayi*. Note the very large pulmonary vein (pv), which collects efferent haemolymph and conveys it to the pericardial cavity. A large vessel on the inner dorsal margin of the lung distributes afferent haemolymph (arrows) (figures and legends reprinted with permission from Greenaway and Farrelly, 1990).

TABLE 3. Ventilatory frequency of some selected decapods from aquatic, amphibious and terrestrial habitats. Showing the tendency to decreased rate when breathing air.

Species	Resting Rate (beat.min^{-1})	Source
AQUATIC		
Cancer magister	75	McMahon *et al.*, 1979
Cancer productus	70	deFur and McMahon, 1984a
Cancer pagurus	82	Bradford and Taylor, 1982
Callinectes sapidus	94	Booth *et al.*, 1982
AMPHIBIOUS		
Cardisoma guanhumi	75 (AIR)	Burggren *et al.*, 1985
Gecarcoidea lateralis	161 (AIR)	Taylor and Spencer-Davis, 1981
	264 (WATER)	
Sudanonautes aubryi monodi	2 (AIR)	Cumberlidge, 1986
	46 (WATER)	
TERRESTRIAL		
Birgus latro	30	Smatresk and Cameron, 1981
Coenobita clypeatus	2	McMahon and Burggren, 1979
Holthuisana transversa	9*	Greenaway *et al.*, 1983a
Pseudothelphusa garmani	1#	Innes *et al.*, 1987

*Employs a 'lung pump' #Some evidence for 'lung pumping'

(*Coenobita*, Morris and Bridges, 1986; *Holthuisana*, Morris *et al.*, 1988a) to between -0.3 and -0.5 for several terrestrial species of *Geograpsus* and *Gecarcoidea* (Morris, Greenaway, McMahon and Sanders, unpubl.). Amongst the Amphipoda, the semi-terrestrial *Talitrus saltator* (Spicer *et al.*, 1990) and *Orchestia gammarellus* (Taylor and Spicer, 1986) produced coefficients of 0 and -0.33 respectively. Calcium sensitivity calculated from data for semi- and fully terrestrial isopods (Sevilla and Lagarrigue, 1979) indicate values ranging from -0.28 to +0.53. The significance of this Ca effect, while appreciated for amphibious/semi-terrestrial species (above), remains to be determined in terrestrial species.

The temperature sensitivity of O_2 transport warrants some consideration. In a number of semi-terrestrial/supratidal species the temperature sensitivity is reduced near to the environmental mean (*O. saratan* $\delta H = -3$ kJ.mol^{-1}, *C. clypeatus* -14.8 kJ.mol^{-1}; Morris and Bridges, 1985, 1986) and may reflect the varying temperatures that occur in beach areas. In contrast the arid-zone crab *H. transversa* also potentially experiences fluctuating temperature but shows no special adaptation of the Hc ($\delta H = -54$ kJ.mol^{-1}) but instead may avoid temperature extremes during the aquatic and fossorial phases of its life cycle. The semi-terrestrial amphipod *Talitrus saltator* shows a marked temperature sensitivity and Spicer *et al.* (1990) also suggest that cryptic and fossorial phases enable this species to escape temperature extremes which have promoted low temperature sensitivity (-11 to -21 kJ.mol^{-1}) in a range of supratidal amphipod Hcs (Taylor and Spicer, 1986). The majority of truly terrestrial species inhabit tropical/sub-tropical rainforests which are characterised by remarkably constant temperature and high humidity. *Geograpsus crinipes*, *G. grayi*, *Gecarcoidea lalandii*, *G. natalis* and *Birgus latro* all taken from the rainforest of Christmas Island all show high temperature sensitivity, at least up to 30°C (Morris *et al.*, 1988b; Morris, Greenaway, McMahon and Sanders, unpub.), whereas *Grapsus tenuicrustatus* and *Geograpsus stormi* taken from shore rocks, beach rubble and cliff faces show much lower sensitivities (-21 and -1.5 kJ.mol^{-1}). The tentative conclusion is that minimising the effect of temperature on blood O_2 transport is as important to terrestrial species from eurythermal habitats as to inter- and supratidal species. In general the blood of air breathers has become increasingly independent of biochemical modulators and instead the animals appear to rely on morphological and mechanical compensation mechanisms.

Dehydration could present a problem for air breathing species. Data from the high-shore *Cy-*

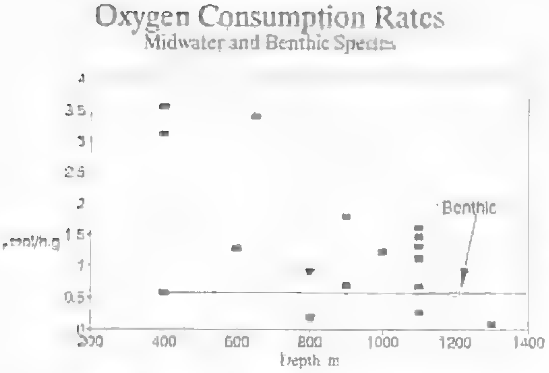


FIG. 7. Oxygen consumption rates from a variety of non-migrating pelagic species indicating reduced O_2 uptake in the deeper dwelling species. The O_2 uptake rate of benthic species appears to remain relatively constant and independent of depth (horizontal line). The rates for pelagic and benthic forms coincide near 1200 m (data from Childress, 1975; Mickel and Childress, 1982b; Childress and Mickel, 1985).

clograpsus lavauxi suggest that under normal circumstances loss of body water does not affect O_2 uptake (Innes *et al.*, 1986). Severe dehydration of *Coenobita clypeatus* appears to reduce O_2 consumption, without significant effects on CO_2 excretion, although the reasons for this are unclear (McMahon and Burggren, 1988). Dehydration is likely to be important only under exceptional circumstances but requires further investigation.

OCEANIC SPECIES

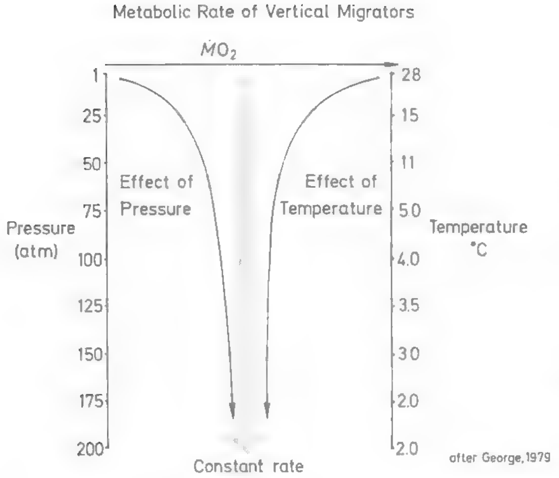
Oceanic crustaceans can be divided on the basis of habitat, sublittoral, pelagic and benthic. Vertically migrating species experience very different temperatures, oxygen availability and pressures at different depths. Benthic species and non-migratory pelagic species live at near constant temperatures and high pressure. The benthic species include the rather special case of the hydrothermal vent fauna which, in addition to high sulphide and metal levels in the water, tolerate high and widely varying temperature as well as high pressure.

There have been relatively few studies of the effect of temperature on oxygen uptake rates of oceanic species. Pelagic crustaceans living in midwater environments tend to show increased rates with temperature, with Q_{10} values of 1.5 to 3.0 (Teal, 1971; Childress, 1977). It is now well established that deep-living pelagic crustaceans have considerably lower O_2 uptake rates than do shallower-living pelagic species (Childress and Mickel, 1985), often by a factor of 20 but that this effect declines below 1500 m (Fig. 7). This decline is more than can be accounted for by temperature effects and cannot be explained by pressure (Mickel and Childress, 1982a). Childress and Mickel (1985) suggest that it is the relaxation of selection for strong swimming abilities at greater depth that allows for a reduced O_2 demand.

In migratory species the response to temperature is influenced by oxygen availability and hydrostatic pressure. The ecological significance of temperature-pressure interactions was shown by Childress (1977) working on the migrating copepod, *Gaussia princeps*. This species was most sensitive to pressure at shallow depths (100 – 300 m) during the night but that during the day, below 400 m within the oxygen minimum layer temperature determined rates. A lowered rate of oxygen uptake while in a hypoxic environment would be of direct benefit. On the basis of such studies Vernberg (1983) supports the model of George (1979; Fig. 8). This suggests that vertical migrators maintain a constant oxygen uptake as a result of the opposing effects of temperature and pressure changes. Deeper in the oxygen minimum layer environmental PO_2 may become very low (<20 torr) and oxygen potentially limiting. Midwater species appear to be adapted to this situation, however, and most exhibit critical oxygen tension (*Pc*) below that normally encountered in the oxygen minimum layer (Childress, 1975; Table 1). This seems to be achieved by maintaining a high flow of water over the gills, which have unusually high surface area and a high diffusion capacity (~10 fold greater normal) leading to a low δPO_2 across the gills (Belman and Childress, 1976).

There are few deep-living brachyuran species and very few studies of benthic Crustacea. Existing data indicate that there is no decrease in the O_2 consumption of benthic species in dependence of habitat depth (Childress and Mickel, 1985). Interestingly, the O_2 consumption rates of midwater and benthic species converge at about 1200 m (Fig. 7).

Respiratory gas transport in oceanic crustaceans has been infrequently examined but Arp and Childress (1985) examined the blood of a benthic (1800 m) shrimp, *Glyphocrangon vicaria*. The oxygen binding properties of this species do not appear too exceptional, with a modest Bohr shift (ϕ = -0.37, 2°C), a relatively low affinity (P_{50} = 9.0 torr, pH 8.01, 2°C) and

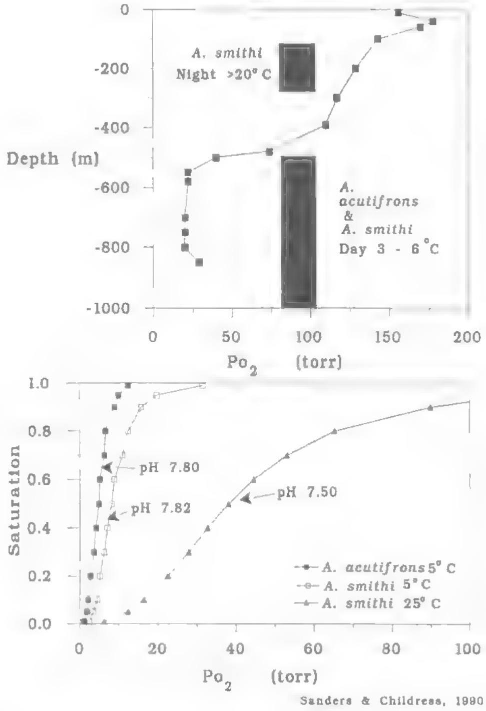


after George, 1979

FIG. 8. Demonstrating, using the model of George (1979), how the opposing effects of increasing pressure and decreasing temperature on the metabolic rate of vertically migrating crustaceans can operate to produce a constant rate throughout the water column.

relatively low co-operativity (n_{50} = 2.6 – 3.2). An unusual aspect of the haemolymph from benthic species is the marked increase in the Bohr factor (pH sensitivity) at higher temperatures, which has also been observed in the brachyuran *Hyas coarctatus* (Morris and Bridges, 1989). The oxygen affinity of haemocyanin from these species is remarkably insensitive to temperature, for *G. vicaria* δH = -10.3 kJ. mol^{-1} (calculated from Arp and Childress, 1985) and -6.4 kJ.mol^{-1} for H. coarctatus (Morris and Bridges, 1989). The normal sensitivity would be nearer to -35 kJ.mol^{-1} (Bridges, 1986, table 3). It is possible that considering these animals usually occur in cold, stenothermal environments that these changes with increased temperature do not have any physiological significance.

In terms of modulator sensitivity there seems to be no special adaptation to life in the deep ocean, for example *G. vicaria* has little sensitivity to L-lactate ($\delta \log P_{50} / \delta \log [lac]$ = -0.04) while *H. coarctatus*, which does extend in shallower water shows a greater sensitivity (-0.17). In recent investigations Sanders and Childress (1990a) have examined the oxygen transport function of Hc from a group of pelagic species, some vertical migrators. The migratory species had lower oxygen affinities but higher *in vivo* lactate levels than the non-migratory species. These shrimp Hcs exhibited, however, very little sensitivity to L-lactate and temperature seems much more important. The non-migratory species had low temperature sensitivity (δH = 0 to -5.6 kJ.mol^{-1}, cf. *G. vicaria* above) whereas there were very large temperature sensitivities in the migrators (δH = -135 to -140 kJ.mol^{-1}). Sanders and Childress (1990a) suggest that low temperature sensitivity is not a feature of benthic crustaceans alone but rather of deep living forms, in stenothermal environments. They also conclude that increased O_2 affinity at lower temperatures is adaptive, by maintaining O_2 uptake, for migrating species as they move down into the relatively cold and hypoxic oxygen minimum layer. In the warmer surface waters, where



Sanders & Childress, 1990

FIG. 9. Adaptation to the oxygen minimum layer. The upper panel shows the decrease in water oxygenation that occurs with increased depth (solid symbols) and the depth ranges for *Acanthephyra smithi* and *A. acutifrons* (shaded blocks). *A. acutifrons* is a non-migrating species that remains in the relatively cold oxygen minimum layer. *A. smithi* can be found within the same range during the day but at night moves into shallower water which has a higher temperature and PO_2 . The lower panel shows the oxygen equilibria of the two bloods at *in vivo* pH. Note that although *A. smithi* has a relatively low affinity pigment suited for the warmer oxygenated surface waters at depth the pigment functions much like that of the permanent inhabitants of the O_2 minimum layer (after Sanders and Childress, 1990a).

the animals are active at night, the reduced affinity will aid unloading at the tissues while loading is maintained by the relatively high PO_2 of the water (Fig. 9).

There are some deep-sea pelagic species such as *Notostomus gibbosus* that maintain their station in the water column not by swimming but by being buoyant (Sanders and Childress, 1988). This shrimp has replaced large amounts of Na^+ with trimethylamine (113 mmol.L^{-1}) and ammonium (217 mmol.L^{-1}) to achieve neutral buoyancy but these normally toxic ions have significant effects on blood pigment functioning (Sanders, Morris, Childress and McMahon, in prep.). The presence of these ions greatly reduces the affinity of the Hc for oxygen, markedly depresses co-operativity and completely suppresses the Bohr shift so that affinity remains constant with changing pH (Fig. 10). Considering that other mesopelagic species also contain these ions further investigation of Hc function under these conditions is required. However, it may be that in an animal where blood pH is determined by factors other than the respiratory CO_2 and anaerobic lactic acid production, that a pH insensitive pigment is advantageous.

Hydrothermal vent crustaceans while difficult and costly to study are of special interest due to the unique nature of their island habitats. The vent brachyuran, *Bythograea thermydron*, shows oxygen consumption rates in the normal range for shallow water brachyurans and does not show unusual temperature sensitivity of O_2 uptake (Mickel and Childress, 1982b). Oxygen binding by the haemocyanin of *B. thermydron* is, however, distinctly unusual (Sanders *et al.*, 1988). In *Bythograea* an increase from 2 to 10°C causes an affinity increase ($\delta H = +23$ kJ.mol^{-1}) but from 10 to 20°C behaves normally ($\delta H = -60$ kJ.mol^{-1}). This was in contrast to the blood of the vent caridean *Alvinocaris lusca* which exhibited a reverse temperature effect over the entire temperature range, so that affinity was lower at low temperature ($\delta H = +13$ kJ.mol^{-1}; Sanders *et al.*, 1988). The Bohr shift in *A. lusca* is twice that of *B. thermydron* (the Bohr shift is dependent on the hydrothermal vent site; Sanders, pers. com.) suggesting that in *A. lusca* significantly decreased affinity *via* a low pH will enhance O_2 delivery to the tissues. *B. thermydron*, with a low pH sensitivity, experiences decreased O_2 affinity at low and high temperature. At low temperatures the Q_{10} effect will reduce oxygen demand. As temperatures increase nearer to the vent water PO_2 decreases and *Bythograea* responds with pronounced hyperventilation (Sanders *et al.*, 1988) which is the normal response of shallow water brachyurans to hypoxic stress and results in an exceptionally low P_c (Mickel and Childress, 1982b); which should be compared with rock pool species (Table 1). This species also has pronounced anaerobic metabolic capacity for short hypoxic forays (cf. intertidal species) and interestingly L-lactate has a potentiating effect on the haemocyanin of this species, which is again reminiscent of shallow water forms. What is unusual is that thiosulphate, the detoxified product of vent sulphide, in *Bythograea* also increased Hc oxygen affinity (Sanders and Childress, in prep.). *B. thermydron* shows some specific adaptations to the variable temperature of its habitat but shows no unusual adaptations to pressure and retains the aquatic brachyuran response to hypoxia.

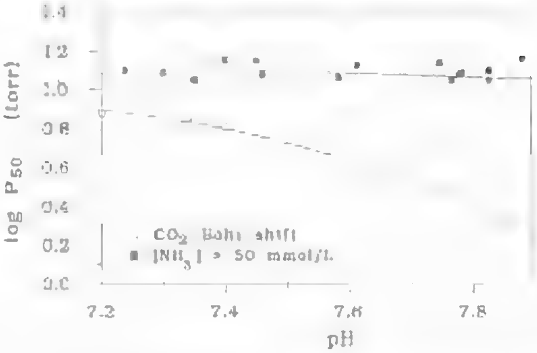


FIG. 10. The oxygen affinity (log P_{50}) of haemocyanin from the mesopelagic shrimp *Notostomus gibbosus* is shown to behave normally with respect to pH but the affinity and pH sensitivity are significantly modified by the presence of high concentrations of NH_4+ and NH_3. Under *in vivo* conditions of high ammonia and trimethylamine the oxygen affinity is both much lower and insensitive to pH (Sanders, Morris, Childress and McMahon, unpubl.)

To conclude, the Crustacea show a range of sophistication of respiratory gas exchange and transport. Adaptations occur at the cellular and enzyme level with respect to temperature sensitivity in order to regulate O_2 demand and CO_2 production, and are exhibited by species from various habitats. Environmental hypoxia is met either by a lowering of the P_c, by improving oxygen uptake efficiency and regulating demand; or by a behavioural response, air breathing. The emergence response may represent the first steps towards terrestrialism. Aquatic and proto-amphibious species take advantage of a range of metabolites to regulate haemocyanin oxygen affinity and this appears to have evolved from an exercise response. Some freshwater, intertidal, vertically migrating pelagic and vent species which experience varying temperature show adaptation of haemocyanin function. Species from more stable temperature regimen, both aquatic and terrestrial, show fewer adaptations in respect of temperature. Fully terrestrial species show marked changes in the morphology of the gills and especially the branchiostegal membrane.

The evolution of a lung has allowed the Crustacea to take advantage of the relatively greater concentration of O_2 in air but in the most adapted species has made them obligate air breathers. Terrestrialism is correlated with a decreased utilisation of biochemical modulation of blood gas transport and an increased importance of morphological and mechanical compensation mechanisms. While there exist clear trends within habitats and obvious transitional adaptations between habitats there are also unusual cases, e.g. thiosulphate in vent crabs and high NH_3 in some mesopelagic shrimp, that are met by unique adaptations. While it has not been possible to devote space to the special case of parasitic species it would be interesting to determine if increased dependence on a host for respiratory gas exchange released parasitic forms from the selective pressures and adaptations described in the paper.

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